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A CHROMATOID BODY SIMULATING AN ACCESSORY CHROMOSOME IN PENTATOMA.

EDMUND B. WILSON.

A brief account will here be given of a body that first attracted my attention in the spermatogenesis of *Pentatoma* (*Rhytodolomia*) *senilis* Say, where it offers so deceptive a resemblance to an accessory or unpaired *X*-chromosome that it might readily lead to erroneous conclusions could not its entire history be followed out in every detail. A body that is evidently of the same nature but somewhat smaller was afterwards found in *Pentatoma* (*Chlorochroa*) *juniperina* L., and in *Podisus crocatus* Uhler, where it is still smaller. A similar body is often seen also in *Cœnus delius* Say, but appears here to be of less constant occurrence. Its behavior is essentially the same in all these cases, and I suspect that it will be found in many other insects. It is probably of the same general nature as the bodies that have been described by various observers as "chromatoid Nebenkörper," "chromatoid corpuscles," etc., in the spermatogenesis of vertebrates, insects, and other animals. In *Pentatoma senilis* it is of very large size, invariably present, and almost always single, though one or two similar but smaller granules often appear also in the same cell. Its constancy and conspicuous character in this species exclude the possibility of error in its identification at any period save the earliest.

As seen during the growth-period and the spermatocyte-divisions it is of rounded form, dense and homogeneous consistency, and after double staining with hæmatoxylin or safranin and light green is at every stage colored intensely blue-black or brilliant red, precisely like the chromosomes of the division-period or the chromosome-nucleoli of the growth-period. In the first spermatocyte-division it may lie anywhere in the cell, sometimes almost at the periphery, but is often close beside the chromosomes. In the latter case it usually lies in, on or near the spindle, lags behind the chromosomes during the anaphases,

and in later stages is found near one pole, presenting an appearance remarkably like that of an accessory chromosome (Figs. 8–10). For such in fact I at first mistook it, even after the discovery that a similar body is often also seen near one pole in the *second* division (Figs. 22, 23); for I supposed this might be a case like that of *Ascaris megalocephala*, where, according to Edwards ('10) the *X*-chromosome may pass undivided to one pole in either the first or the second division. The resemblance is indeed most deceptive; and these division-figures have often been exhibited to other observers as "a remarkably clear demonstration of an accessory chromosome" without at first arousing the least suspicion of the hoax.

The body in question is nevertheless neither an accessory nor any other kind of chromosome; though this did not become wholly certain until after a study of the entire spermatogenesis. It is in fact of protoplasmic origin, first appearing early in the growth-period outside the nucleus, whence it may be followed uninterruptedly through all the succeeding stages until it is finally cast out of the spermatozoön. Upon dissolution of the nuclear membrane it is left lying near the chromosomes, passes without division into one of the daughter-cells in each of the spermatocyte-divisions, and thus enters but one fourth of the spermatids. In the latter it persists with little or no change until a very late stage, sooner or later wanders far out into the sperm-tail, and is at last cast off altogether. It therefore takes no visible part in the formation of the spermatozoön.

I have as yet been able to study the testes of only a single individual of *P. senilis:* but since the whole history of the chromatoid body is clearly shown in this material the facts will be described because of the emphasis that they place on certain possible sources of error in the study of the numerical and sexual relations of the chromosomes. One of the testes was fixed in Flemming's fluid (the best fixation), one in Bouin's, and both were at first stained in iron hæmatoxylin. One of the Flemming slides was also stained in light green: this slide was afterwards extracted and successfully restained with safranin and light green, giving a preparation of great brilliancy. The results given by these four methods of staining are entirely consistent. In all cases

the chromatid body is intensely and purely stained by the "nuclear" dye. In the Flemming material the intranuclear plasmasome, sharply defined and uniformly present, is after hæmatoxylin alone pale yellowish, after both double stains clear green. In the Bouin slides, as is often the case with material thus fixed, the plasmasome stains with hæmatoxylin almost as intensely as the chromosome-nucleolus, and in the earlier part of its history is often indistinguishable from the latter. Unsuccessful attempts were made to restain the Bouin slides with the Biondi-Ehrlich and the Benda (mitochondrial) methods. With the latter, both chromosomes and chromatoid bodies stained alike with the crystal violet after every degree of extraction. With the former method, neither of these bodies could be made to hold the methyl green, both staining alike clear red. I think it probable, however, that with suitable fixation these two kinds of bodies could be differentiated by one or the other method.

I.

Without additional material, including smear-preparations, the interesting history of the chromosomes can not be completely elucidated, owing to certain difficulties in the early and middle prophases. With exception of these stages however the relations of the chromosomes are shown with a diagrammatic clearness that leaves nothing to be desired; and they will be briefly described, both for their own sake and because this is necessary to a complete demonstration of the behavior of the chromatoid body.

The spermatogonial groups (Figs. 1–3) contain six chromosomes, the smallest number thus far recorded in any heteropteran (in *P. juniperina* the number is 14, as in *Euschistus*). Two of these may always be recognized as the largest. Of the remaining four two, as the subsequent history proves, are the *X*- and *Y*-chromosomes; but these differ so slightly in size that they can hardly be distinguished with certainty at this time. The first spermatocyte-division may be described as showing in polar view four chromosomes (Figs. 4–6), including one large (*B*) and one small bivalent (*b*), and the univalent *X*- and *Y*-chromosomes; but the latter lie close together, often in contact, and not seldom

are so closely associated that they might well be reckoned as forming a single tetrad. In the second division *X* and *Y* are uniformly coupled to form a bivalent (Figs. 14, 15); hence but three chromosomes appear in polar view (Fig. 13), and each spermatid receives this number.

The relations of these chromosomes in the spermatocyte-prophases and in the first division show some very interesting features. The autosomes (bivalents) are always characterized by their quadripartite or tetrad structure, being deeply constricted transversely, and also longitudinally cleft, sometimes so markedly that in polar view each appears distinctly double (Figs. 5, 6, 19, 20). This cleft, extremely conspicuous in the prophases, is often less marked during the metaphase, but is again conspicuous in the anaphases, when each daughter-chromosome is always distinctly double, as may be seen with diagrammatic clearness in polar views (Figs. 11, 12). The *X*- and *Y*-chromosomes, on the other hand, are always bipartite and only form a quadripartite body when the two are in contact or closely associated. In the middle prophases they lose their compact, nucleolus-like form and become more or less elongated, looser in texture, and they are now conspicuously split lengthwise, but show no sign of transverse division. In later prophases, as all the chromosomes condense, they shorten more or less but still retain, as a rule, the form of longitudinally split rods at the time they enter the metaphase group. They are at this time frequently in contact end to end (Fig. 17), but *may be quite separate*, though always near together. Their later history is shown in Figs. 18, *a–f*, all of which are accurately represented in the same position with reference to the spindle (in correspondence with Fig. 17). Of this series of figures, *a* and *b* are from metaphases, the others from anaphases. This series, every stage of which is shown in numerous cases in the preparations, clearly demonstrates that the original longitudinally split rods progressively shorten, and that the two halves of each are then drawn apart at right angles to the original long axis. Each chromosome thus assumes a dumbbell shape (*a–c*) and finally divides "transversely"; but it is certain from the earlier stages that this division is only the completion of an original longitudinal split. When *X* and *Y* are closely

associated (as in *a* and *b*) they may be described as forming an actual tetrad, the first division of which is evidently equational.

An excellent opportunity is afforded by these stages for critical comparison of the relative sizes of *X* and *Y*. Such a comparison, made in a large number of cells, shows that a slight but evident inequality almost always exists, the fact being placed beyond doubt by its appearance in both daughter-pairs (Figs. 18, *d–f*). The inequality is however not always seen, perhaps because of slight differences of form or foreshortening. In respect to the size-differences between *X* and *Y*, *Pentatoma senilis* seems to approach *Oncopeltus fasciatus*, as described in my eighth "Study," and differs markedly from *P. juniperina*, where the difference is as evident as in *Euschistus*.

Among numerous cases examined I have not found an exception to the rule that *X* and *Y* lie near together, often more or less in contact, and divide in this position. This relation is maintained during the anaphases, so that in the final stages *X* and *Y* form a pair that is hardly to be distinguished from the small bivalent autosome, now always distinctly double (Figs. 11, 12). Each secondary spermatocyte thus receives three pairs of chromosomes, two of which are the longitudinally divided daughter-autosomes and the third the *XY*-pair. These three double elements enter the second division spindle directly, without forming a "resting-nucleus," and each is separated into its two components (Figs. 14–16). This of course involves the disjunction of *X* and *Y*. In this division the inequality between these chromosomes is almost always in evidence, the appearance of the *XY*-pair being somewhat similar to that of *Nezara hilaris*, as described in my seventh "Study."

It would be hard to find a more convincing demonstration than is here afforded of the relation between univalents and bivalents in the maturation-divisions (*cf.* Wilson, '12) or of the fact that the bivalent is equivalent to two univalent dyads united together. Were the association of *X* and *Y* only a little closer they would in fact form an actual tetrad essentially like the autosome tetrads. Considering the *XY*-pair as such, it evidently divides longitudinally (equationally) in the first division and in the second undergoes a typical reduction-division (disjunction of *X* and *Y*).

Despite the small number of chromosomes I have not been able to understand completely their history during the early and middle prophases, when their elongate form and close apposition to the nuclear membrane renders their complete analysis in sections very difficult. Smear-preparations alone, I believe, will fully clear up the facts. In the middle prophases (Fig. 31) the chromosomes are characterized by the exaggerated character of the longitudinal split (as compared with other insects I have examined) the two halves being often quite as widely separated as in the copepods (Häcker and his followers). Their number at this time often appears to be *five* (instead of the expected number, four), and in some cases even six, the diploid number. This puzzling fact I can not yet fully explain; but it appears to be due to the very wide separation of the two moieties of one or both bivalents at the point where each is destined to undergo "transverse" division in the first spermatocyte-mitosis. It is at any rate certain that this is characteristic of the large bivalent during the earlier period of its condensation, when it often gives the appearance of two separate, longitudinally split chromosomes, separated by a considerable space, and only connected by two delicate strands (Fig. 19, *a*). That this pair represents the large bivalent is fully established by later stages, in which all intermediate conditions connect it with the large bivalent of the metaphase figure (Fig. 19). The same is certainly true in some cases also of the small bivalent (Fig. 20); but I am not sure of the constancy of this. These facts raise the question whether a very late end-to-end conjugation may not take place, in a manner analogous to that described by Gross ('04) at an earlier period in *Syromastes*. The investigation of this point in smear-preparations will probably yield interesting results.

We now return to the history of the chromatoid body. No sign of it is seen in the spermatogonia, nor can it be positively identified in the spermatocytes until some time after the synizesis. But already in the stages immediately following synizesis, as the chromosome-threads are beginning to spread through the nuclear cavity, from one to three very small, deeply staining granules make their appearance in the protoplasm, usually not far from the nucleus, each of which may often be seen to lie in a clear,

vacuole-like space (Fig. 26). In slightly later stages *one* of these granules rapidly enlarges and may soon be distinguished as the chromatoid body (Fig. 27). The other granules seem in many cases to disappear, though they may often be distinguished in addition to the large chromatoid body up to a late stage and even during the divisions (Figs. 29, 30, 10). No evidence can be found that any of these granules are extruded from the nucleus (as has been suggested for the "chromatoid Nebenkörper" by several earlier observers); and it may be pointed out that throughout all these stages both kinds of nucleoli are always clearly visible within the nucleus. Neither can I find evidence of any connection between them and the centrioles, which are first seen in much later stages, lying close against the nuclear membrane.

The chromatoid body reaches its maximum size in Stage *f* or the "confused period" (Fig. 30) when it becomes a most conspicuous element which from this time forward undergoes little or no change until long after its delivery to the spermatids. During this whole period it is always surrounded by a clear, vacuole-like space, and may thus be identified at every stage, even during the divisions. The examination of hundreds of cells during this whole period in *P. senilis* has shown only two or three cases in which more than one such large chromatoid body is present. Its single character seems therefore to be typical of this species. In *P. juniperina*, on the other hand, two such bodies, equal or unequal in size, are more often seen.

From the early post-synaptic stage forwards the nuclei always contain a well defined, conspicuous plasmasome, and one or two intensely stained chromosome-nucleoli. When single, the chromosome-nucleolus is about twice the size shown when two are present (Figs. 26–30). In the earlier stages these bodies are often more or less irregular in form, or elongated. In later stages they are nearly spheroidal, and appear exactly similar, but for their position, to the extra-nuclear chromatoid body. During the prophases the plasmasome disappears, while, as already stated, the chromosome-nucleoli are converted into chromosomes of looser texture, somewhat elongated, and like the bivalents conspicuously split lengthwise. In the final prophases all the

chromosomes become condensed and stain intensely, while the chromatoid body is unchanged (Figs. 32–34). Upon dissolution of the nuclear membrane the latter is left nearly in its original position, often close beside the chromosomes, but still always distinguishable from them by the surrounding vacuole. In the anaphases it usually lies rather close to the spindle, often directly upon it (Fig. 10), sometimes actually embedded within it (Figs. 8, 9) as may be proved by careful focusing. It may however lie quite outside the spindle, even near the cell-periphery. In any case it passes bodily into one of the secondary spermatocytes. There are of course two classes of the latter, with and without the chromatoid body (Figs. 22–25); in the former class its history in the second division repeats that seen in the first. The result is that it enters but one fourth of the spermatids, where it lies in the protoplasm outside the nucleus, and owing to its undiminished staining capacity long remains the most conspicuous object in the cell.

The structure and history of the spermatids agrees in the main with the descriptions of Henking, Paulmier, Gross and Montgomery for other Hemiptera, and need not be described in detail. Each spermatid contains besides the nucleus a large, spheroidal chondriosome-body or nebenkern, a much smaller pale sphere from which arises the acrosome (Figs. 36, 37) and (after the earlier stages) a rather large, intensely staining centriole lying close against the nuclear membrane, from which the axial filament grows out (Figs. 38–43). The later history of these structures agrees closely with Montgomery's account of *Euschistus* ('11). In the earlier stages the chromatoid body, when present, may lie at any point, more commonly in front of or behind the nucleus. Whatever be its original position it is sooner or later, without exception, carried far out into the outgrowing tail of the sperm-cell. It may often still be seen near the anterior pole of the spermatid, near the acrosome-sphere, after the latter has performed its first migration to the anterior pole (Fig. 39) but may lie near the opposite pole (Fig. 40). When the sphere again moves backwards towards the posterior pole of the nucleus the chromatoid body moves with it (Fig. 41) and is never again seen near the anterior pole. By the time the acrosome-sphere has

again moved forward to its definitive position at the anterior pole of the nucleus the chromatoid body is always in the tail (sometimes much earlier), often at a considerable distance from the head.

As the elongation of the tails proceeds, the chromatoid body is carried still further away from the head, finally reaching a position in the middle tail-region. When the nuclei have become elongate, homogeneous and intensely staining, and the immature spermatozoa are aggregated in parallel bundles, the chromatoid bodies are still conspicuously seen (particularly well in the safranin-green preparations) scattered irregularly within the bundles of sperm-tails. They are at this time still enclosed within the tails, lying in the protoplasm outside the chondriosome-envelope of the axial filament; but their elimination shortly takes place. This process is preceded by a marked accumulation of protoplasm that forms a swelling at one side of the tail within which the chromatoid body lies (Figs. 44, 45); but similar swellings are also seen in the spermatids that contain no chromatoid bodies. That these protoplasmic masses are sloughed off in both cases is certain from the ensuing and final stage, though in my rather scanty material I have never been able to catch the process in the very act. In the succeeding stages numerous protoplasmic balls are found lying between the tails (usually more or less definitely aggregated near the middle tail-region of the bundle) and quite separate from them (Fig. 46). It may now be seen with perfect clearness that the chromatoid bodies have been cast off with the protoplasmic balls; for they are now never within the tails but are still perfectly evident in many of the free protoplasmic balls. Counts of the latter show that the chromatoid body is present in about one fourth of them. It still stains as intensely as ever, and is often quite unchanged, but in many cases has now assumed a crescentic shape, as if the central cavity had broken through to the exterior at one side (Fig. 45).

These facts seems to admit of no other interpretation than that a considerable mass of protoplasm is sloughed off from each spermatid, and that it carries with it the chromatoid body when present. It is certain that the latter does not contribute in any visible way to the formation of the spermatozoön.[1]

At every period of its history the chromatoid body is often homogeneous in appearance; but not infrequently it shows more or less definite indications of a central cavity. Here and there one may be found in which the cavity is clearly evident; and now and then a definite, sharply stained central granule appears within the cavity (Figs. 21, 43). This granule has only been seen in the dividing spermatocytes and in the spermatids. Since centrioles are also seen in these stages they are evidently not derived from the central granule of the chromatoid body.

Apart from its smaller size, the chromatoid body in the three other species mentioned shows the same general history as in *P. senilis*. In *P. juniperina* it is at its maximum size hardly more than half as large as in *P. senilis* (Figs. 34, 35); it is very often accompanied by a much smaller and paler granule lying close beside it (Fig. 35). In *Podisus crocatus* it is somewhat smaller than in *P. juniperina* (Fig. 33), in *Cœnus delius* still smaller and might readily be mistaken for an accidental granule. In all these cases its behavior seems to be of the same type, and it is surrounded by a similar vacuole. In the two forms last mentioned, perhaps because of its small size, its position in the divisions is more variable, and it more often lies away from the spindle or near the periphery of the cell.

II.

The nature of the chromatoid body need not here be considered *in extenso*. As before stated, it is probably of the same nature as the "chromatoid Nebenkörper" described by various observers in other animals; but I know of no case where the facts are in all respects identical with those seen in *Pentatoma*. In the rat, for example, the "chromatoid Nebenkörper" as described by v. Lenhossék ('98) is in some respect remarkably like that of *Pentatoma:* but this body (two are often present in the earlier

[1] The elimination of protoplasm from the spermatid is of course a well-known and widespread phenomenon. In the cockroach, as described by Morse ('09) the process appears to be similar to that seen in *Pentatoma*, and here also a deeply staining body is cast off, which Morse identifies as a plasmasome. I think it possible, however, that this too may be a chromatoid body comparable with that of *Pentatoma*. I also think it probable that the bodies that have been described as "degenerating cells" in the late spermatid-cysts by some observers are identical with the protoplasmic balls here described.

stages) is stated to be present in all the secondary spermatocytes and also in all the spermatids, where its maximum size is attained. Duesberg ('08) found it only after the first division and believed "qu'il persiste pendant la mitose et se divise pour son propre compte," though the division was not actually seen. Both observers agreed that it degenerates in the spermatid (*cf.* also Meves, '99). Regaud ('10) again describes it in the rat, but finds that it fragments into small granules during the first division and is afterwards reconstituted to form a single body which passes to one pole in the second division, beyond which stage its history was not traced. Such a process of fragmentation certainly does not take place in *Pentatoma*, nor can there be the least doubt of its absence from the greater number of spermatids.

I suspect that the body described by King ('07) as an "acrosome" in the spermatogenesis of *Bufo* belongs in the same general category, though it is described as having a very different history from that seen in either the insects or the mammals. Lastly, I may point out the probable identity of the chromatoid body in *Pentatoma* with that described by Doncaster ('10) in the gall-fly *Neuroterus*, which likewise passes to one pole in the spermatocyte-division. This observer tentatively suggests a possible connection between this body and sex-determination; but the facts seen in the Hemiptera evidently lend no support to this. In none of these cases is the real nature of this body yet clear. In *Pentatoma* it is obviously not a centrosome, centriole, acrosome or extruded nucleolus. Since no definite idiozome is seen in the spermatocytes I suspected for a time that it might be such a body; but this too seems to be excluded by the conditions described in the mammals, where an idiozome is also present.

The nature of the chromatoid body thus remains problematical, but the facts are worthy of serious attention for another reason. Were the chromosomes very small, numerous, closely crowded, or otherwise unfavorable for exact study, and could not the entire history of the chromatoid body be so clearly traced, even an experienced observer might fall into the most confusing error concerning the relations of the chromosomes. It may seem superfluous to urge the danger of confusing with chromosomes other compact and deeply staining bodies that may lie near or

among them, or at the spindle poles—extruded nucleoli or nucleolar fragments, chromatoid bodies, "acrosomes," yolk-granules, or the like—but one can not avoid the suspicion that some of the existing contradictions in the literature may have arisen from some such source. Many cases might be cited in illustration of the danger of such confusion. I suggest, for instance, a comparison of my Figs. 9, 10, 22, 23 of *Pentatoma* (first and second division) with Stevens's Fig. 5 of the first division of *Ceuthophilus* ('12), the same author's Fig. 71 of *Stenopelmatus* ('05), Morse's Fig. 46 of *Periplaneta* ('09), and Duesberg's Fig. 45 of the rat ('08). In all of these cases a compact, more or less deeply stained, spheroidal body is seen near one pole in the telophases or late anaphases, lying near the chromosome-group; and the similarity is increased by the fact that in the first three of these cases this body is surrounded by a clear, vacuole-like space. So deceptive is this resemblance that any observer without careful study might readily conclude that the body in question is in each case an accessory chromosome; yet in only two of the five cases would this conclusion be correct. In *Pentatoma* and the rat this body is of protoplasmic origin (chromatoid body), in *Periplaneta*, according to Morse, an extruded nucleolus (plasmasome). Only in *Ceuthophilus* and *Stenopelmatus*, if Miss Stevens's conclusions were correct (I have no reason to doubt that they were) is this body an accessory chromosome.

Such facts make it clear that the presence of sex-chromosomes can not safely be inferred alone from the presence of chromosome-like bodies lagging on the spermatocyte-spindles, or lying near one pole. The presence of compact, deeply staining nucleoli during the growth-period is by itself equally indecisive. In some cases the "plasmasome," especially after certain fixatives such as Bouin's fluid, may stain quite as intensely as the chromosome-nucleoli with hæmatoxylin, safranin and other dyes (*cf.* Gutherz, '12). Decisive evidence regarding these bodies can only be obtained by tracing their individual history and by accurate correlation of the chromosome-numbers in the spermatogonial and spermatocyte-divisions. It hardly need be added that great caution is necessary in dealing with difficult material in which for any reason such a test can not be completely carried out.

COLUMBIA UNIVERSITY, February 19, 1913.

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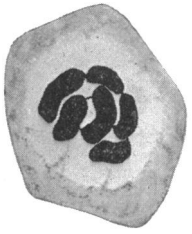
Explanation of Plates.

Plate I.[1]

(*Pentatoma senilis.*)

Figs. 1–3. Spermatogonial metaphase-groups; 4–6, first spermatocyte-division in polar view; 7, early anaphase, the large bivalent also shown separately at the left; 8–10, late anaphases; 11, 12 the same in polar view, sister-groups from the same spindle (the identification of *X* and *Y* not entirely certain); 13, second spermatocyte metaphase-group, with chromatoid body; 14–15, the same in side view, chromatoid body absent; 16, the same, with chromatoid body near one pole.

[1] All the figures from camera drawings, enlarged about 2,500 diameters. *A* designates the acrosome, *B* the large bivalent, *b* the small bivalent (or their products), *C* the chromatoid body, *N* the Nebenkern or chondriosome-body, *X* and *Y* the sex-chromosomes.



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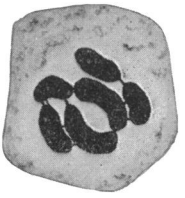

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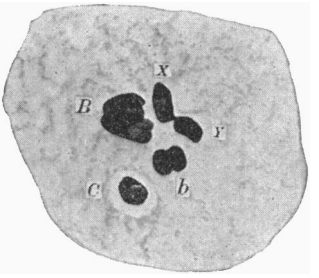

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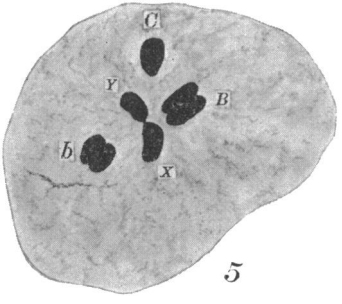

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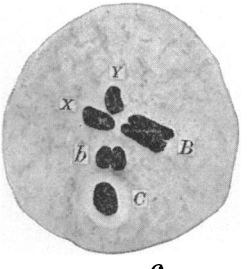

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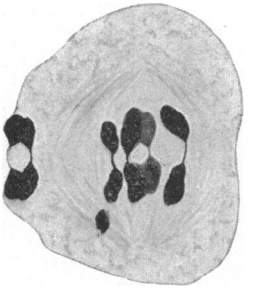

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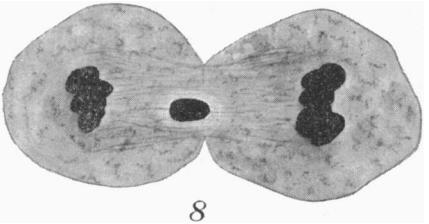

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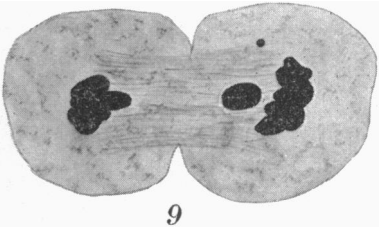

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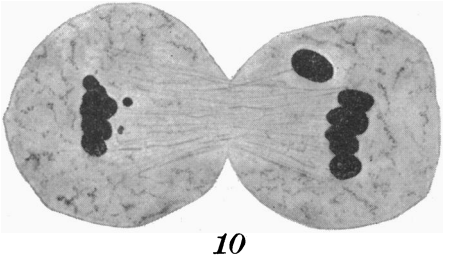

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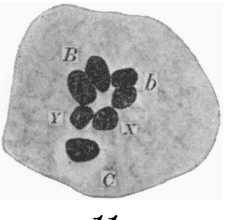

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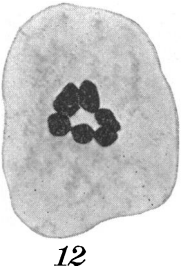

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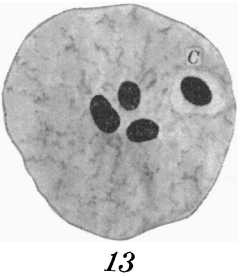

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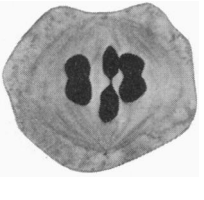

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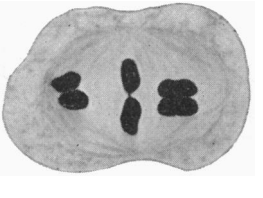

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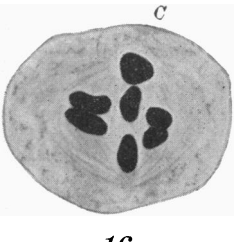
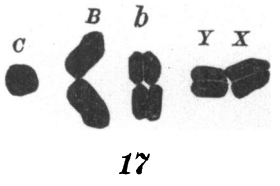


16

PLATE II.

(*Pentatoma senilis*, except 25.)

FIG. 17. First spermatocyte-metaphase chromosomes from a single spindle, with chromatoid body, artificially spread out in a series for comparison, the large bivalent seen sidewise; 18, *a–f*, the *XY*-pair in successive stages, all in the same position with reference to the spindle (as in Fig. 17), *a* and *b* from metaphases, *c–f* from anaphases; 19, *a–e*, the large bivalent in successive stages, *a–d* from prophase-nuclei, *e* from metaphase; 20, *a–e*, corresponding series of small bivalent, *a–c* from prophase-nuclei, *d*, *e*, from metaphases; 21, tangential section of first division showing *XY*-pair and chromatoid body; 22, 23, second spermatocyte-telophases, with chromatoid body; 24, the same without chromatoid body; 25, the same with chromatoid body near one pole, *Pentatoma juniperina;* 26–29, early growth-period; 30, confused period; 31, middle prophase; 32, late prophase, all the chromosomes foreshortened.



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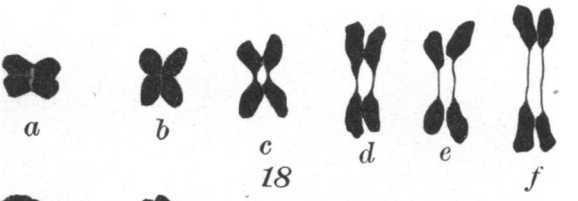

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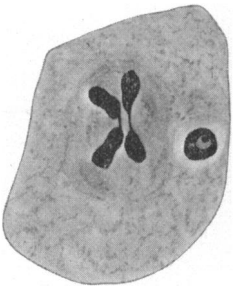

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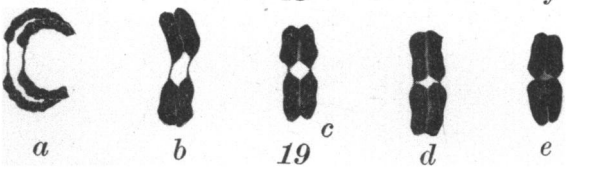

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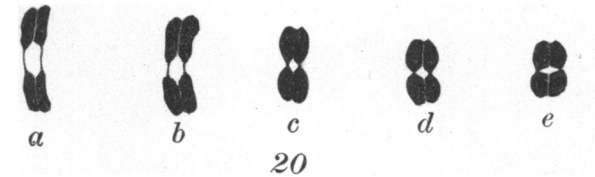

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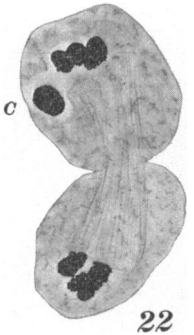

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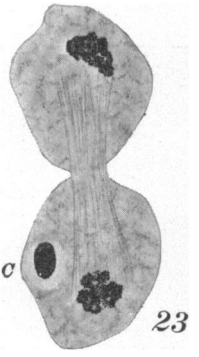

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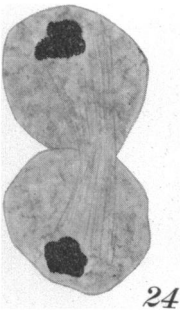

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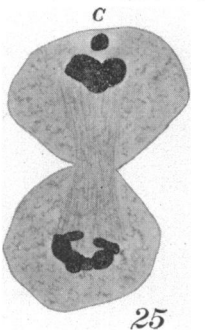

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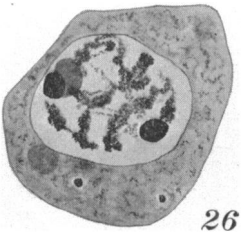

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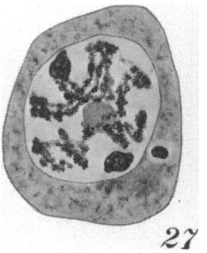

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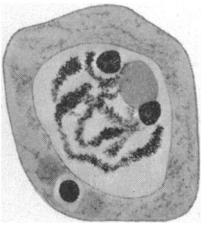

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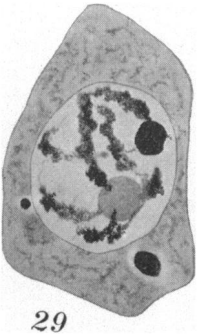

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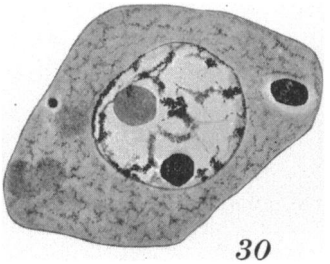

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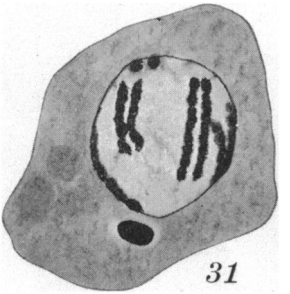

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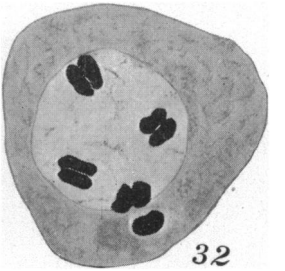
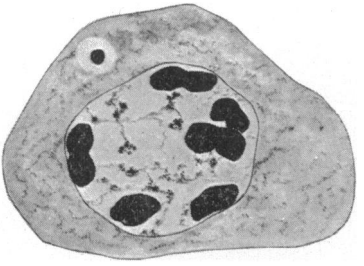


32

PLATE III.

(*Podisus crocatus*, 33; *Pentatoma juniperina*, 34, 35; *P. senilis*, 36–46.)

FIG. 33. Late prophase, *Podisus crocatus*; 34, the same, *Pentatoma juniperina*; 35, first spermatocyte-anaphase of the same species; 36–43, stages in the development of the spermatids, *P. senilis*; the large dark body is the chromatoid body; 44, 45, central region of the tail, later spermatids, showing protoplasmic swelling enclosing chromatoid body; 46, group of cast-off protoplasmic balls lying between the sperm-tails, four containing chromatoid bodies, young spermatozoa.



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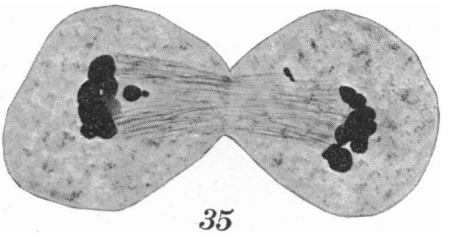

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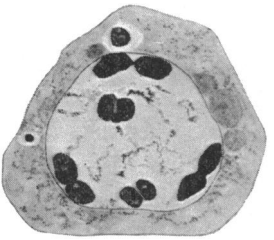

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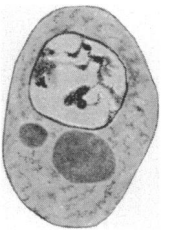

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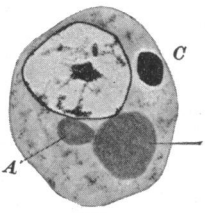

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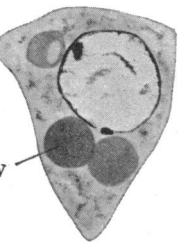

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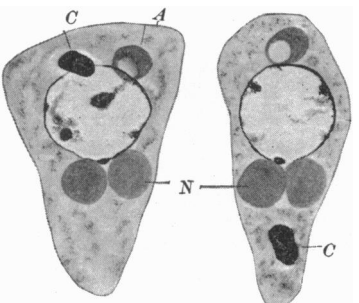

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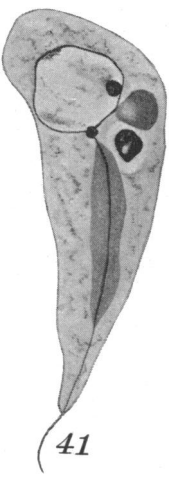

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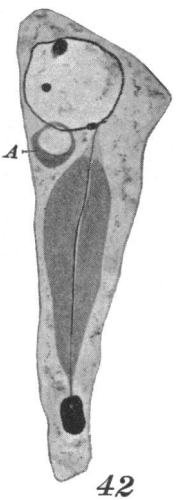

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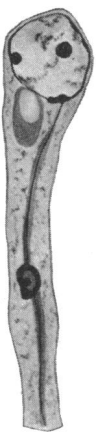

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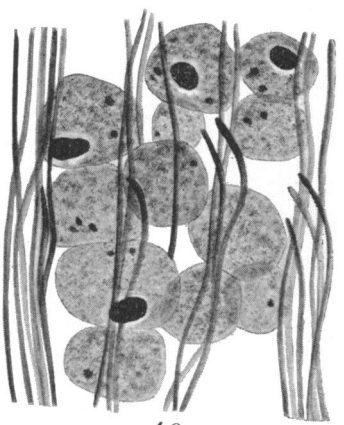

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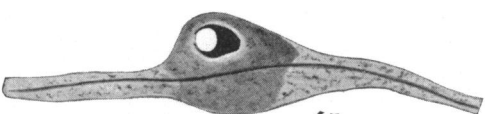

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